Food Preferences, Food Availability and Food Resource Partioning in Two Sympatric Species of Cephalaspidean Opisthobranchs

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(1 Text figure)

INTRODUCTION

Extensive studies of the food resources and the feeding habits of cephalaspidean opisthobranchs are uncommon. With the exception of Paine's (1963, 1965) studies of *Chelidonura* and Burn & Bell's (1974a, 1974b) work on 2 species of *Retusa*, most data concerning cephalaspidean feeding habits have been incidentally reported in papers documenting other aspects of their biology. Such reports indicate that cephalaspideans feed on a variety of epifaunal and infaunal organisms. Hurst (1965) reported that *Philine aperta* (Linnaeus) had fed on Foraminifera and small gastropods and that *Scaphander lignarius* (Linnaeus) had ingested Foraminifera, young urchins, tectibranch gastropods, small bivalves and the polychaete *Pectinaria*. The guts of *Cylichna cylindracea* (Pennant) and *C. magna* Lemche were reported by Lemche (1956) to contain Foraminifera, as were the guts of *Retusa chrysoma* Burn and *R. pelyx* Burn by Burn & Bell (*opp. cit.*), *R. obtusa* (Montagu) by Hurst (*op. cit.*) and *R. ovoides* (Mil.), *R. truncatula* (Bruguière) and *R. variabilis* (Mil.) by Bacescu & Caraion (1956). Along with Foraminifera, small gastropods were also recorded among the gut contents of *R. truncatula* and *R. chrysoma*. Hurst (*op. cit.*) and Burn & Bell (1974b) appear to be the only 2 papers reporting observation of foraminiferan ingestion by cephalaspideans.

As a result of extensive benthic sampling in Monterey Bay by the Moss Landing Marine Laboratories, a large number of specimens of 2 co-occurring cephalaspidean opisthobranchs, *Acteocina culcitella* and *Cylichna attonsa* was available for study. Since these 2 species regularly co-occurred in the same habitats, shared similar anatomical characteristics and, in exploratory dissections, appeared both to feed upon Foraminifera, the present study was undertaken to analyze their food habits and to relate them to food availability. Specifically, we were interested in investigating how 2 such similar species could coexist and how they divided up the food resource.

MATERIALS AND METHODS

The specimens analyzed in this study were collected from 3 stations in northern Monterey Bay, California. The stations were designated as follows: Station 1105: lat. 36°51.0'N; long. 121°49.8'W; depth 16.5 m; Station 1152: lat. 36°54.8'N; long. 122°01.0'W; depth 36.0 m; Station 1177: lat. 36°53.6'N; long. 121°57.5'W; depth 34.5 m. The locations are also shown on Figure 1. These stations were sampled at roughly 3-month intervals from August 1971 through November 1972.

The specimens were collected with a Smith-McIntyre grab which had a sampling area of 0.1 m^2 (Smith & McIntyre, 1954). During the first sampling period (August 1971), 8 replicate samples were taken at each station. During the remaining sampling periods (November 1971, February, May, August, and November 1972), 6 replicates were taken at all the stations except 1105.

Each grab sample was sieved through 1 mm Nytex screens using filtered sea water. The specimens were relaxed with magnesium chloride ($MgCl_2$) and stained with rose bengal in order to differentiate living from dead specimens. Each sample was preserved in 10% buffered formalin and later transferred to 70% ethanol.

Specimens of *Acteocina culcitella* and *Cylichna attonsa* were individually dissected to analyze for any food remains in their digestive tracts. Because of the small size of the opisthobranchs, all examinations were performed under a dissecting microscope. Before dissection, all specimens of *A. culcitella* were measured for greatest shell length.

Using an ocular micrometer, Foraminifera obtained from the cephalaspidean digestive tracts were also measured.

In order to compare the Foraminifera ingested by the snails with the Foraminifera available in the sediment, the 3 stations were again sampled on 21 May 1974. As before, each station was sampled with the Smith-McIntyre grab using the same procedures described above. In addition, each station was also sampled using a Phleger corer (3.6 cm inner diameter). In the laboratory, each core was kept vertical and then sliced into 1 cm sections which were stained with rose bengal and preserved with ethanol. In this way, the vertical distribution of living Foraminifera within the sediment could be determined. Each 1 cm subsample was thoroughly dried in an oven (65° C) and the Foraminifera were separated from the sediment by using a solution of bromoform ($CHBr_3$) in which the specific gravity had been adjusted to 2.2 by the addition of methanol. GIBSON & WALKER (1967) have shown that, at this density, bromoform is consistently more effective in separating Foraminifera from sediment particles than is carbon tetrachloride. Similar results were reported by SEN GUPTA (1971) who recovered 99% of the available Foraminifera with bromoform (diluted with acetone), but only 50 - 85% with carbon tetrachloride.

Overlap in food utilization between the 2 species was calculated using indices R_o, C_λ, derived from information theory as described by HORN (1966). Niche breadth was calculated from formulae of LEVINS (1968).

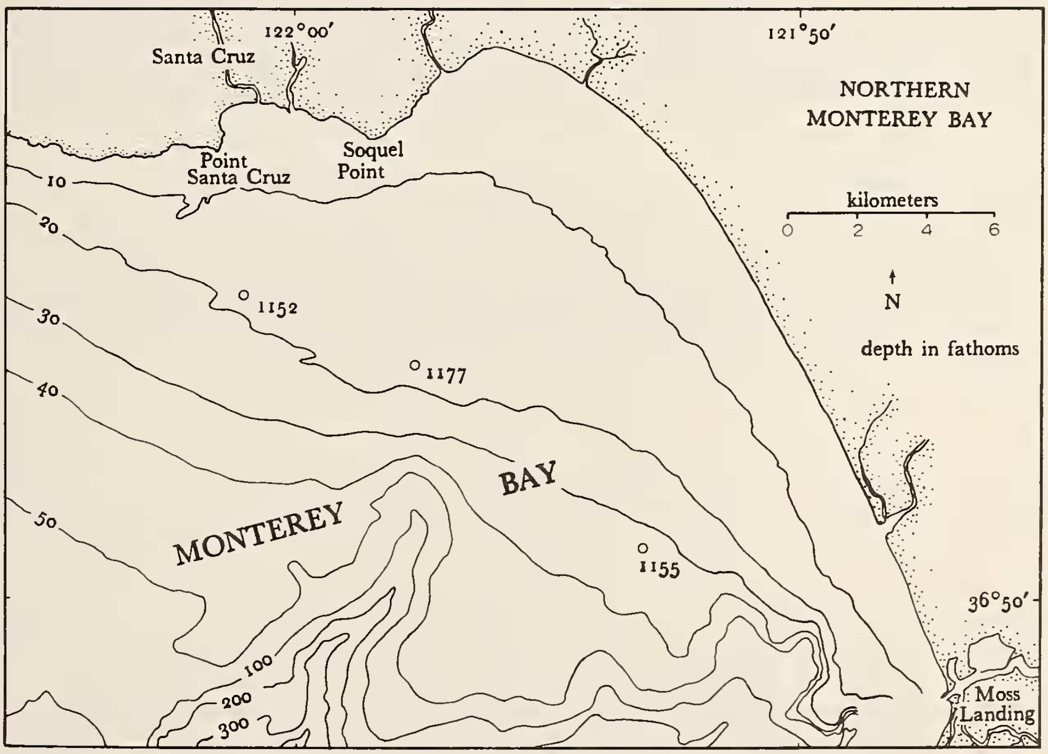

Figure 1

Map of Northern Monterey Bay, California showing location of the three sampling stations

Table 1

Number of Food items Recovered from Digestive Tracts of *Acteocina culcitella*

Prey Item	8/71	11/71	2/72	5/72	8/72	11/72	5/74	Total
Station 1152 N = 125								
Foraminifera								
Haplophragmoides sp.			4	2	5		1	
Trochammina inflata		3	7	4	3		4	
Quinqueloculina sp.		8	15	9	9	1	3	
Triloculina sp.		1	1	2	4			
Miliolid spp.		5	11	5	9	1	3	
Buccella frigida		9	12	22	24		8	
Elphidiella hannai		2	2		5		1	
Elphidium sp.			4		4	2	1	
Globobulimina pacifica						2		
Nonionella sp.			1		1			
Other Invertebrates			6	4	3			
No. Snails Examined		10	45	27	13	9	21	125
Station 1155 N = 54								
Foraminifera								
Alveolophragmium advena			2					
Haplophragmoides sp.		2	5	2				
Trochammina inflata		3	4	2				
Quinqueloculina sp.		13	18	17	2		4	
Triloculina sp.		8	1	2				
Miliolid spp.		14	9	12	3		2	
Bucella frigida		23	8	96	3		15	
Elphidiella hannai		7	6	12			3	
Elphidium sp.		1	2	1				
Fissurina sp.				16				
Nonionella sp.		1	1	2				
Other invertebrates			1					
No. Snails Examined		12	28	9	1		4	54
Station 1177 N = 42								
Foraminifera								
Trochammina inflata	4			3	3		2	
Quinqueloculina sp.	11	5		5	3			
Triloculina sp.	3	2			2		1	
Miliolid spp.	4	7		4	1		2	
Buccella frigida	4	22		43	3		18	
Elphidiella hannai	2	2		4				
Elphidium sp.	2			2				
Fissurina sp.	3			2				
Globobulimina pacifica				2				
Lagena sp.	1			1				
Nonionella sp.				9	1			
Other Invertebrates				1	1			
No. Snails Examined	4	11		13	8		6	42
							Total	221

RESULTS

Food Analysis

1. *Acteocina culcitella*

A total of 221 specimens of *Acteocina culcitella* (Gould, 1853) were dissected to recover food items from the gut. Of these, 93 (42%) had ingested Foraminifera representing species of the 3 common foraminiferal suborders Miliolina, Rotalina and Textulariina. The results are given in Table 1. Foraminifera were recovered from all portions of the digestive tract, but were primarily found in the crop, gizzard and intestine. Those recovered from the intestine occurred both separately and encased within fecal pellets. Ingested rotaliid and textulariinid tests showed no obvious signs of physical or chemical damage. The tests of miliolid Foraminifera, however, often appeared damaged or broken, especially when recovered from the intestine. Miliolids are often described as "porcellaneous" (Cushman, 1969) because their tests have a smooth, shiny appearance which is quite different from the appearance of rotaliid Foraminifera. Broken tests, therefore, could be recognized as "miliolid," even though they might not be identifiable to genus or species. In most cases, the tests of these damaged Foraminifera remained intact as discrete entities, so each could be counted as a separate foraminiferan. These appear here under the heading "unidentified miliolid" or miliolid sp.

The foraminiferan most commonly ingested was the rotalid *Buccella frigida* (Cushman). On several occasions (May, 1972, 1974), *B. frigida* accounted for more than 50% of all the Foraminifera ingested by *Acteocina culcitella* (Table 1). At other times (November 1971, May 1974) at certain stations, miliolids comprised 40 to 60% of all ingested Foraminifera. *Quinqueloculina* sp. formed 82% of the undamaged miliolids, while the remaining 18% were *Triloculina* sp. Several other species of Foraminifera were recovered, though in relatively small numbers. Of these, *Trochammina inflata* (Montagu), a textulariinid whose test is composed of agglutinated sediment particles, was the most numerous (Table 2).

A small percentage of the items ingested by *Acteocina culcitella* were not Foraminifera, but were representatives of 3 different invertebrate phyla: Annelida, Arthropoda, and Mollusca. Neither the molluscan shells nor the ostracod tests were crushed or broken.

2. *Cylichna attonsa*

Analysis of 456 specimens of *Cylichna attonsa* (Carpenter, 1865) showed that 169 (37.1%) had ingested Foraminifera. With but 7 exceptions, these Foraminifera were all of the genus *Nonionella* Cushman. Most were identi-

Table 2

Number of Food Items Recovered from Digestive Tracts of *Cylichna attonsa*

Prey Item	8/71	11/71	2/72	5/72	8/72	11/72	5/74	Total
Station 1152 N = 219								
Foraminifera								
Nonionella basispinata	3		9	10	9	3	8	
Nonionella stella	7		8	7	3	2	6	
Nonionella sp.	5		6	7	3	2	3	
No. Snails Examined	35		50	36	33	40	25	219
Station 1155 N = 146								
Foraminifera								
Nonionella basispinata		14	18	12	11	4	2	
Nonionella stella		1	3	1	2		4	
Nonionella sp.		5	3	3	5	2	2	
Other Material			3		1			
No. Snails Examined		29	40	36	30	3	8	146
Station 1177 N = 91								
Foraminifera								
Nonionella basispinata	3		1	9	6	2	3	
Nonionella stella	6			2	8		1	
Nonionella sp.	2		1	4	3	4	1	
Other Material				1	2			
No. Snails Examined	13		7	25	33	8	5	91
							Total	456

fied as either *N. basispinata* (Cushman, Moyer) (50%) or as *N. stella* (Cushman, Moyer) (22%). The remaining 23% were too small for specific identification and are listed as *Nonionella* sp. These data are displayed in Table 2.

As with the rotaliids taken from *Acteocina culcitella*, those taken from *Cylichna attonsa* showed no obvious signs of chemical or physical damage, even when recovered from the gizzard or beyond. Of the 7 Foraminifera which were not *Nonionella*, 5 specimens were *Buccella frigida* (Cushman) and 2 were *Elphidiella hannai* (Cushman).

Food Availability

The abundance and vertical distribution of Foraminifera collected with the phleger corer were analyzed. These were compared with Foraminifera recovered from the digestive tracts of *Acteocina culcitella* and *Cylichna attonsa* taken at the same stations 1152, 1155, and 1177.

The vertical distribution of living Foraminifera within the top 4 cm of sediment at Stations 1152, 1155, and 1177 on 21 May 1974 is shown in Table 3. In all cases, only the Foraminifera from the top 4 cm are shown because Foraminifera decreased markedly below a depth of 4 cm and because our initial observations suggested that the 2 mollusks could not burrow below 4 cm. At stations 1155 and 1177, 97.1% and 93.1%, respectively, of all Foraminifera occurred within the first 4 cm, while at Station 1152, 77.7% are within the top 4 cm and 96.1% of all Foraminifera are found by the 5th centimeter. Within the first 4 cm, no distinct pattern of stratification could be discerned, either in the number of individuals or in species composition. The highest number of Foraminifera occurred within the 0 - 1 cm increment at Station 1155, the 2 - 3 cm increment at Station 1177 and the 3 - 4 cm increment at Station 1152. Similarly, the highest number of foraminiferal species occurred within the first cm of substrate at Stations 1155 and 1177, but within the 1 - 2 cm and the 3 - 4 cm increments at Station 1152. Certain species occurred at only one level (*e. g.*, *Bolivina* sp., *Globobulimina pacifica* and *Nonionella fragilis*), while others (*e. g.*, *Nonionella basispinata* and *Buliminella elegantissima*) occurred at all 4 levels.

Table 3

Distribution and Abundance of Foraminifera in the Top 4 cm of Substrate at 3 Stations

	Sta. 1152 (2 cores) Increment (cm)				Sta. 1155 (1 core) Increment (cm)				Sta. 1177 (2 cores) Increment (cm)				Total Per 4 cm		
Species	0-1	1-2	2-3	3-4	0-1	1-2	2-3	3-4	0-1	1-2	2-3	3-4	1152	1155	1177
Haplophragmoides sp.			0;2		8	4	1						2	13	0
Textularia sp.				1;1	1						1;1	1;0	2	1	3
Trochammina inflata				26;14					2;2		1;3		40	0	8
Pelosina sp.					6	4	5	5					0	20	0
Protcornina sp.					4			2					0	6	0
Quinqueloculina sp.	3;2	0;1		1;1		1	4		2;2		2;1		8	5	7
Buccella frigida		1;0			47	13	22	13	4;6				1	95	10
Bolivina sp.					1								0	1	0
Buliminella elegantissima		8;4	3;1						2;4	1;1	15;11	4;10	16	0	48
Elphidella hannai	1;1	1;1	2;2		3		3			7;8			8	6	15
Globobulimina sp.						1							0	1	0
Nonionella basispinata	1;1	3;4	5;11	1;3	20	5	11	7	0;1		8;3		29	43	12
Nonionella fragilis		7;12			3								19	3	0
Nonionella globosa			1;1	2;1									5	0	0
Nonionella stella		20;15	8;14	2;2	3	4	2			1;1		1;1	61	9	4
Total Per cm															
Core 1	5	40	14	32	96	32	48	27	10	8	27	6			
Core 2	4	37	31	22					15	9	19	11			
$\bar{X}$/Core	4.5	38.5	22.5	27					12.5	8.5	23	8.5			
Total Per 4 cm															
Core 1	91				203				51						
Core 2	94								54						

DISCUSSION

The diets of 2 sympatric cephalaspidean opisthobranchs are reported herein for the first time. Both are demonstrated to feed upon Foraminifera. MURRAY (1973) has suggested that Foraminifera may be ingested by 2 types of feeder, unselective predators who ingest sediment which contains Foraminifera, and selective predators who preferentially seek out Foraminifera.

Analyses of the food items recovered from the guts of both *Cylichna attonsa* and *Acteocina culcitella* suggest that neither can be placed in the category of unselective predators. The 2 species ingest different food items, even though the same food resources are available to both. *Cylichna attonsa* is extremely stenophagous and feeds only upon foraminiferans of the genus *Nonionella*. Foraminiferans of the genus *Nonionella* comprise from 3.3 to 23.6% of the individuals in the top 4 cm of the core samples from the 3 sampling stations, but in no case are they the most abundant foraminiferan in the sample. They are, however, second in abundance rank at Stations 1155 and 1152 and 4th at Station 1177. *Cylichna attonsa*, therefore, is a specialist concentrating upon one of the abundant foraminiferan genera. Such extreme stenophagy suggests that the abundance of *Nonionella* does not vary much over the course of the year. Unfortunately, we lack data on abundance of the foraminiferan fauna for other seasons of the year.

Acteocina culcitella, on the other hand, is more of a generalist, feeding upon 13 different species of Foraminifera as well as taking a few other small invertebrates. If *A. culcitella* were an unselective predator, it would be expected that the food items in the guts of the cephalaspidean would be in the same abundance as in the substrate samples. A series of Spearman rank correlation tests comparing the abundance of the foraminiferans in the diet with those in the substrate were all insignificant ($P > 0.05$), indicating that at all 3 stations *A. culcitella* does not take food in relation to abundance. Hence, this species, although a generalist, is a selective predator.

The Foraminifera which were the highest in abundance in the guts of *Acteocina culcitella* were *Buccella frigida* and *Quinqueloculina* sp. In the top 4 cm of the substrate at the 3 stations, *B. frigida* was first in abundance only at Station 1155, whereas at Stations 1152 and 1177, it ranked 11th and 4th, respectively. *Quinqueloculina* sp. ranked 6th in abundance at Station 1152, 8th at Station 1155 and 6th at Station 1177. This is further evidence that *A. culcitella* does not take prey in relation to its abundance in the substrate.

To see whether *Acteocina culcitella* changed its diet with respect to season, we made tests comparing the rank abundance of prey items in the diet among the sampling dates for the 3 stations. In all cases, there were significant correlations in rank abundance of prey between any 2 sampling dates (Spearman rank test, $P < 0.05$, all comparisons). This suggests that either there is no difference in the composition of the prey over season, or that *A. culcitella* maintains its dietary preference in the face of changing abundances of prey organisms, since the significant rank correlation values mean that there is a very low probability that the 2 sets of values compared could have come from different populations.

Because the 2 opisthobranch species differ markedly in the prey species which they ingest, there is very little overlap in the diets of the 2; hence, the low values of the overlap index shown in Table 4. We conclude, then, that no significant competition occurs between these 2 species with respect to food.

Table 4

Overlap Values for Diets of *Cylichna attonsa* and *Acteocina culcitella* at 3 Stations and Niche Breadth for *Acteocina culcitella*

	Station 1152			Station 1155			Station 1177		
Date	C_λ	R_o	1/B	C_λ	R_o	1/B	C_λ	R_o	1/B
Aug 1971							0	0	4.05
Nov 1971				0.028	0.091	2.01			
Feb 1972	0.036	0.095	4.64	0.072	0.249	4.43			
May 1972	0	0	2.58	0.019	0.119	2.27	0.245	0.497	2.53
Aug 1972	0.029	0.103	4.04	0.134	0.276	1.92	0.162	0.283	5.11
Nov 1972	0	0	2.78						
May 1974	0	0	3.53	0	0	1.93	0	0	1.34

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